STUDIES ON A PHOSPHORESCENT BERMUDAN ANNELID, ODONTOSYLLIS ENOPLA VERRILL.

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I. INTRODUCTION AND NATURAL HISTORY.

During the summer of 1904 the senior author, while working at the Bermuda Biological Station, had the opportunity to observe with some care two appearances of a remarkably interesting phosphorescent annelid.* The laboratory was at that time located at Hotel Frascati on the Flatts Inlet to Harrington Sound. The tide runs freely into and out of the Sound by way of the Inlet. The worms appear periodically in the waters of this inlet in considerable numbers and with striking regularity. It was reported to me that they also occur in the waters of St. George's Harbor. In all likelihood they are to be found at numerous points about the Islands.

Two appearances were observed by me at Frascati, and a third was reported to me. The first occurred July 3-7, with a maximum on the 4th; another July 29-31, with a maximum on the 30th. The latest appearance was reported to me as occurring on August 23; but details are lacking as to its duration. There is thus an interval of about 26 days between these maxima.

The full meaning of this interval is not clear. The lunar month is, however, at once suggested. This would in all probability come to be established through the tides, either alone and directly, or in connection with light variations produced by tidal variation. These agencies might possibly become operative in two ways: (1) in connection with the formation of the sexual cells, and (2) in their

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release. How the effects are wrought in this case we are not in a position to say. The matter should receive more careful local study.

According to the tide tables, the tide was at its lowest for the day in the Bermudas on July 4 about 6:30 P. M., the moon being in its last quarter on July 5th. On July 27th was a spring tide; and the second recorded appearance began July 29th. On July 31 there was a near-spring tide at its lowest daily phase at 7:30 P. M. While these two appearances do not show a strict parallelism with the lunar phases, they do involve a coincidence of low tides and approaching dark.

If my informant was correct in his dates, the third appearance would occur at high tide. It is possible that the first appearance of the season, involving a release of gametes, is stimulated by low tide or by the coincidence of low tide and approaching dark; that the time necessary for renewal of reproductive bodies has been established at approximately the lunar month by a series of circumstances, internal and external; and that the release of the sexual products occurs on the first approach of dark after their maturity irrespective of the height of the tide at the time.

Parallel instances of periodicity in the formation and release of sexual bodies are numerous, in which both tide and light appear to play a part.

In addition to the monthly periodicity, there is a daily periodicity. On both occasions on which they were carefully observed they appeared each day, within fifteen minutes of the same time, just as dusk was becoming pronounced.

The display lasted from twenty to thirty minutes. Only a few appeared at first, each evening. The numbers gradually increased to a maximum, when scores might be seen at once. The display waned somewhat more rapidly than it waxed. An occasional belated specimen sometimes appeared some minutes afterward.

In a similar way, not so many individuals were seen on the first evening of each period. On the second or third night they reached a maximum, and again dwindled in numbers on following days.

Of the three appearances, that of early July was the most numerous, and that of August the least so. This suggests an annual,

as well as a daily and monthly maximum; but this needs further observation.

The males and females differ considerably in size—the females often being twice as long as the males. The larger female specimens attain a length of 35 mm. Both sexes are distinctly phosphorescent:—the female with strong and more continuous glow, and the male with sharper, intermittent flashes.

In mating, the females, which are clearly swimming at the surface of the water before they begin to be phosphorescent, show first as a dim glow. Quite suddenly she becomes acutely phosphorescent, particularly in the posterior three-fourths of the body, although all the segments seem to be luminous in some degree. At this phase she swims rapidly through the water in small, luminous circles two or more inches in diameter. Around this smaller vivid circle is a halo of phosphorescence, growing dimmer peripherally. This halo of phosphorescence is possibly caused by the escaping eggs, together with whatever body fluids accompany them. At any rate the phosphorescent effect closely accompanies ovulation, and the eggs continue mildly phosphorescent for a while. The fact that the luminosity is known at no other time is further suggestive that it is produced by the material which escapes from the body cavity. If the phosphorescent glands are external, as the histology of the epidermis at least suggests, the discharge of the glands is closely correlated with ovulation.

If the male does not appear, this illumination ceases after 10 to 20 seconds. In the absence of the male the process may apparently be repeated as often as four or five times by one female, at intervals of 10 to 30 seconds. The later intervals are longer than the earlier. Usually, however, the males are sufficiently abundant to make this repetition unnecessary; and the unmated females are rare, if they are out in the open water. One can sometimes locate the drifting female between displays by the persistence of the luminosity of the eggs; but the male is unable to find her in this way.

The male appears first as a delicate glint of light, possibly as much as 10 or 15 feet from the luminous female. They do not swim at the surface, as do the females, but come obliquely up from the deeper water. They dart directly for the center of the luminous

circle and they locate the female with remarkable precision, when she is in the acute stage of phosphorescence. If, however, she ceases to be actively phosphorescent before he covers the distance, he is uncertain and apparently ceases swimming, as he certainly ceases being luminous, until she becomes phosphorescent again. When her position becomes defined he quickly approaches her, and they rotate together in somewhat wider circles, scattering eggs and sperm in the water. The period is somewhat longer on the average than when the female is rotating alone; but it, too, is of short duration.

So far as could be observed, the phosphorescent display is not repeated by either individual after mating. Very shortly the worms cease to be luminous and are lost. Often they give the appearance of sinking out of sight; however, this appearance is negatived by the fact that I have caught both sexes at once by timing the current and dipping down stream, as much as six or eight feet from the point of latest visible phosphorescence. Sometimes as many as two or three males seem to take part in one mating.

The females caught and examined immediately on becoming luminous are full of eggs. Those caught after three or four displays, or after copulation, are largely empty of eggs; yet the different segments of one worm will differ widely in this particular. Eggs are often caught among the setæ and at any other points where they can be held.

Specimens in confinement after copulation may be aroused into mild phosphorescence for at least an hour.

The group of mating adaptations in this Syllid is peculiarly large and complex; and the elements entering into the precision with which the eggs and sperm are brought together are quite worth notin. In a number of counts made of eggs captured in connection with the copulating worms, I found a range of 45-80 per cent of fertilized eggs in five batches taken at random. Considering the external fertilization of the eggs this must be considered very high. It is quite probable that this is a higher result than would be attained if the eggs and worms had been left in the sea.

The following correlated adaptations are noteworthy:

1. The concentration of the ripening and production of the ova and sperm into a few days of each month, in the worms of a

given locality; and the coincidence of the periodicity of the male and female.

2. The further concentration of these processes into 30 minutes of the twenty-four hours, and at the coming of darkness.

3. The coincidence of the luminosity with the emission of eggs and, so far as we know, its confinement to this period.

4. The repeated periods of luminosity of the female—serving as an adequate lure for the male, even though his distance may be considerable.

5. The sex-dimorphism in the character of the flashes in male and female, which may serve as recognition marks.

6. The fact that the females swim at the surface of the water at this time, while the males are beneath the surface until the former become luminous, enables the males to locate the females with greater precision. This position of the female may also make the oxidation more complete, and thus secure the increased luminosity.

7. The eyes of the male are perceptibly larger than those of the female, in spite of the fact that the females are distinctly larger than the males.

II. CLASSIFICATION.

The Syllidae, of which *Odontosyllis* is a genus, are an interesting and widely distributed family of annelids. While nothing is known of the habits and manner of life of this species of *Odontosyllis* except what is seen in this mating period, there are numerous striking features of the family recorded. They are mostly free-swimming forms; but it is believed that they dwell largely amidst the fixed vegetable and animal growths between the tide-marks, or at shallow depths, and seek their food there. Some species are known to be commensal with sponges. Certain species of *Autolytus* are reported to be parasitic on nemerteans, and other species of Polycheta. In such cases the proboscis is said to be incapable of being retracted.

To the general student the most remarkable facts about the family relate to the methods of reproduction. As in some of the naidiform Oligocheta, the non-sexual reproduction by "budding" is a common occurrence. This budding may be of the nature of transverse fission, as in the naidiform worms; or it may be lateral,

sometimes even with rosettes of buds rising from the side of the body. In one species of *Autolytus* the budding may continue from these primary buds in such a way as to produce a complex, much branched stock very similar to plant growth. As will be recognized, this is an uncommon occurrence among animals as highly differentiated as the Syllids. In *Autolytus* and some other genera, possibly in many of the genera, a non-sexual nurse-stock gives off numerous sexual buds or zooids, which ultimately escape and mate as free-swimming worms. The embryos develop into the nurse-stock and thus a somewhat complicated alternation of generation comes about.

Malaquin (1893) diagnoses the family Syllidae as follows:

"Cephalic segments provided with 5 appendages: Namely, two palpi; two lateral and one median antennæ; and two pairs of eyes. The peristomial (post-cephalic) segment usually has two pairs of tentacle-like cirri,—sometimes only one pair. The succeeding segments have feet consisting only of the setigerous lobe of the ventral division, together with a dorsal and a ventral cirrus. The dorsal division of the foot often develops at the time of sexual maturity. The proboscis is protrusible, and consists of two regions: (1) the anterior (pharynx) chitinous and with one or more teeth; (2) the muscular gizzard, which is a secondary development of the pharynx of the larva. Reproduction is distinguished by the appearance of secondary sexual characteristics (such as enlargement of the eyes, elongation of the antennae, development of swimming bristles and of genital glands, and often of phosphorescent organs). The ordinary individual may thus itself become sexual by these changes (epigamy); or it may give rise to new and special buds which separate and assume the sexual characteristics (schizogamy)."

The Syllidae are divided into the following sub-families:

Syllidae.	Palps present..	Fused.........	Thruout.............	Exogonea.
			At base only.........	Eusyllidae.
		Separate...........................		Syllidae.
	Palps wanting....................................			Autolytea.

Malaquin defines the Eusyllidea, to which *Odontosyllis* belongs, thus:

"Syllidae with ventral cirrus (McIntosh says that these may be absent; they are wholly wanting in both sexes of the worm under consideration); palpi fused at the base only. Tentacular cirri filiform and cylindrical, with surface constrictions. Reproduction epigamous (direct)."

Odontosyllis was established as a genus by Claparede (1863) and is described as follows:

"Palpi short or moderately elongated; more or less separate or fused at

the base. Tentacles (3) and the dorsal cirri filamentous, short—becoming longer in sexually mature zooids. Nuchal organ has a central pit. Tentacular cirri in two pairs. Ventral cirrus present [not in the sexual zooids of *O. enopla*]. Proboscis with a series of horny papillæ, the points curved backward. Ventricle (stomach) short and devoid of T-shaped cæca. Bristles with the terminal piece simple or bifid."

Verrill (1900) has described *Odontosyllis enopla* as follows:

"A large species with a dark brown, wide, short esophagus, armed with a ventral row of six stout, recurved, hook-like teeth anteriorly, besides the median dorsal tooth.

Head large, broader than long, broadly rounded in front and on the sides; posteriorly with two rounded lobes, separated by small median emargination. Eyes black, unequal, the anterior ones much larger, reniform; those of each side are so close together that they seem to be almost in contact.

Palpi shorter than the head, rather wide, thin, often wrinkled or folded in contraction, and commonly curved downward.

Tentacle tapered, rather slender, not annulated, its length about 1½ times that of the head. Antennae similar, about ½ as long. Tentacular cirri similar to the tentacle, the upper one rather larger and longer; the lower ones shorter; first dorsal cirrus decidedly longer and larger than the upper tentacular cirrus. Succeeding ones mostly shorter, unequal, alternately shorter and longer, tapered distally; the longer ones are equal to the breadth of the body, the shorter ones about ½ as long; those on setigerous segments 3, 4, 6, 9 are longer than the others.

The setæ are all similar, numerous, slender, short, projecting but little beyond the parapodia, with short, rather wide blades, ratio as 1:2½-3; their tips are strongly incurved and acute, with a small denticle a little distant from the end. [Fig. 16, V.] Two spiniform yellow acicula usually occur in each fascicle.

The esophagus is short and occupies about 4 segments; its margin is incurved and strongly emarginate dorsally. It bears a group of 6 [see Figs. 18, 19, 23] nearly equal, parallel, recurved hooks or teeth, which are large and strong. The conical dorsal tooth is near the margin.

The stomach is large and occupies 8 segments; it is wide, elliptical, and about twice as long as the esophagus. Its surface is covered with angular or alveolar markings, often hexagonal, so as to have a honeycomb-like appearance, but not arranged in definite rows.

Color, in formalin, is nearly white, except when containing eggs.

Length, 25mm; diameter, about 1.5mm.

One of the largest specimens has all the segments back of the gastric region filled with eggs."

III. GENERAL AND EXTERNAL MORPHOLOGY.

As in the other nereidiform worms, the body is elongated and very mobile. The length varies in the observed specimens from 19

to 35 mm. The males are distinctly smaller than the females. Just back of the head the body is almost cylindrical. The dorsi-ventral diameter grows continuously shorter from before backward, while the transverse diameter lengthens for about 40 segments, after which it too gradually diminishes.

The segments vary in number from about 110 to 130, in the twelve or fifteen specimens examined. They may be grouped in the following regions: (1) a head with 3 to 6 supecialized segments including the first setigerous segment; (2) an anterior body region of 23 or 24 segments, in which there is a gradual increase in the right-left diameter, and upon which the dorsal portion of the parapodium (notopodium) bears no setæ, although the ventral process (neuropodium) does; (3) a mid-region, comprising some 30 to 32 segments, and similar to the last segments of the preceding region but for the fact that each notopodium bears a cluster of long, swimming setæ in addition to the neuropodial setæ; (4) a posterior region, similar to the second region in that the notopodial setæ are lacking, which includes all the rest of the worm, except—(5) the specialized anal segment which bears beside the anus, a pair of elongated cirri. The variation in the number of segments in the worms is due to differences in the fourth region enumerated above. The length of the other regions is subject to very little variation.

The Head.

As is usual in the polychetes the head is well differentiated, and the problem of its segmentation is not an easy one. There is the usual pre-oral portion known as the prostomium; the mouth itself; and a region surrounding the mouth and just back of it, the peristomium. See Figs. 2, 5, 12, 13. This specialized head includes the first setigerous segment and everything in front of it. If the prostomium, as is held by Malaquin, consists of one segment only, the head of *Odontosyllis* contains four segments. If, as Pruvot thinks, the prostomial lobe represents a modification of three segments, there are six segments in the head.

If we regard the prostomium and its outgrowths as fully homologous with the structures in other regions of the body it would seem that Pruvot's contention is the sounder of the two. For the dorsal prostomial lobe bears three types of paired sensory struc-

tures: foremost of all, two ciliated palps; back of these and separated from them by a groove, the pair of lobes bearing the eyes, of which there are two on each side of the head; and, lying between these lobes, the three tentacles, one medium and two lateral (Fig. 12). It is not easy to see how this region can be regarded as segmented at all and consider it of less than three segments; but in the light of the embryonic development of this and similar worms it is questionable whether it is sound to try to homologize the divisions of this prostomial organ or even the whole organ with the segments of the body. In the larva of *Odontosyllis,* as in other Syllids, segmentation is distinctly a secondary state, superimposed on the posterior part only of trochosphere. The anterior enlarged portion seems not to share in this embryonic segmentation. In our opinion the prostomium rather represents a modification of this unsegmented anterior outgrowth of the trochosphere. It is not even morphologically a whole segment; but is rather an outgrowth and specialization of a portion of the first embryonic segment.

The peristome, on the other hand, is clearly of three segments, each bearing a pair of lateral cirri becoming progressively more dorsal. Only the third of these segments (posterior) appears, however, as a complete ring of the body. The dorsal part of this segment may protrude in the form of a flap covering the base of the lobes bearing the eyes (Figs. 1, 13, *F.*). In life this is quite distensible. A ventral projection of this same segment froms the lower lip (Fig. 5). The first and second segments show only as partial rings extending from the side of the mouth to the over-arching prostomium.

The Eyes.

The four eyes are arranged in pairs, two eyes on either side of the median line (Figs. 1, 12, 13, *Ey.*) They are mounted on protruding lobes which are capable of a certain amount of motion. The anterior eyes are somewhat larger than the posterior ones, though not markedly so. The eyes of the males are distinctly larger than those of the females. In measurements of the eyes of two males and three females, after making allowance for differences in planes of sectioning, there is a difference of 10-30 per cent in favor of the males. The opening into the pigment cup (pupil) of the anterior

eyes in the normal position is directed forward and outward; that of the posterior ones, dorsally (Fig. 1, *E*.)

The cuticle which covers the front of the eye is a continuation of that which covers the exterior of the body. The lens is a spherical body lying in the cavity formed by the pigment cup (Fig. 7 *Le*.) It appears to be connected with the cuticle through the opening in the pigment cup, by a slender stalk or pedicel. After fixation the lens shows as a somewhat fibrous substance surrounding at various places roundish bodies which stain with greater intensity. It gives the appearance of a semi-fluid substance, that has been coagulated by reagents, rather than of cells. It stains readily and is rendered somewhat brittle by the usual methods of fixation and treatment.

The remaining regions of the eye—rods, pigment layer, retinal cells, and optic nerve, which form the wall of the cup of the eye are not really four distinct regions, but are continuations and differentiations of one layer of çellular elements. The wall of the cup is formed of numerous long and narrow elements *(ommatidia)* all essentially alike, with the long axes in a radial position. Each ommatidium is a highly differentiated cell (Fig. 8). The outer end of each cell narrows into a nerve fibre which enters into the optic nerve. Near this end the cell has its greatest dimensions and contains a large, conspicuous nucleus. The middle part of each of these cells is covered with a dense pigment (Fig. 8, *Pg*.) The united effect of these pigmented regions lying side by side is to produce the pigment layer which is very conspicuous and appears continuous. The inner part of the cell projects towards the lens as a clear hyaline rod. These rods form the peripheral part of the refracting mass, but are morphologically a part of the retina. The pigmented cup is continuous, except at the dorsal region where it is interrupted by a small circular aperture, the pupil, through which the pedicel of the lens passes.

Parapodia.

In the regions of the body, described above as anterior (2) and posterior (4) the dorsal ramus of the parapodium (notopodium) is specially reduced and rudimentary. It is bilobed, consisting of two short processes or tubercles. The dorsal of these is larger and bears a dorsal cirrus (Fig. 21 *Ci*.) These cirri are chiefly outgrowths of

the epidermal layer of cells; but fibres from the circular layer of muscles pass to their bases. The ventral lobe of the notopodium is a smaller, pointed process, bearing no external structures in this region. In the mid-region of the body this lobe bears a conspicuous bunch of about 40 long capiliform, non-branching setæ, arranged in two parallel rows in the sac (Fig. 10, *S''*), and is supported by an aciculum.

The ventral ramous (neuropodium) is well developed throughout. It consists of the usual larger dorsal and smaller ventral lobes. The dorsal lobe has at its outer extremity a cleft or sac in which the setæ are imbedded. These setæ differ from the dorsal ones in being jointed, having a long stalk with a small incurved appendage (Fig. 16, *V.*). This lobe is also supported by internal acicula which reach the surface (Fig. 21, *A*). The setæ of both kinds sit on the basement membrane of the external epithelium and clearly arise from the modified epithelial cells lining the sac (Fig. 9, *C*). The ventral lobe of the neuropodium is small and does not produce the ventral cirrus usually described as characterizing the Syllidæ.

IV. INTERNAL ANATOMY AND HISTOLOGY.

The Body-wall.

The body-wall is composed of the four usual regions; viz., (1) the cuticle, (2) the epidermis, (3) the muscular system and (4) the parietal peritoneum.

The secreted cuticle is of about the same thickness in all regions, except in a location just anterior to the peristomial flap where it is much increased in thickness (Fig. 6, *E*[1]). It shows the following perforations: (1) the pores of the epidermal glands; (2) the points of emergence of the setæ from the body-wall; and (3) the external openings of the nephridia at the ventral basal region of each parapodium.

The cuticle takes any of the general stains, showing up peculiarly well when treated with haematoxylin. It possesses a characteristic luster which is apparent in all preparations, irrespective of the kind of treatment. Under the highest powers the homogeneous appearance gives way to a suggestion of very fine intersecting lines. The striations perpendicular to the surface are more apparent.

The epidermis is a conspicuous layer of cells in most parts of the body and is easily traceable over the exterior of the body and into the anal and oral openings. The epidermis is composed of three kinds of cells: viz., (1) the ordinary undifferentiated epithelial cells which compose the greater part of the epidermis; (2) the large regular gland cells; and (3) the "twisted" gland cells.

In all parts of the epidermis, with a few exceptions to be noted, the cells of the first class are of the usual columnar type, with conspicuous nuclei near the bases. The basement membrane is very definite in all regions, staining readily with haematoxylin. In certain quite definite regions these cells vary from the common shape. They become much more elongated near the base of the parapodium on both dorsal and ventral sides. The greatest thickening takes place, however, in the region just in front of the dorsal flap, that extends forward from the last peristomial segment, and just at the base of the brain. At this point the epidermal cells are tremendously elongated—the length in the longest being something like fifteen times the short dimension, and 6 or 8 times as long as is usually the case (Fig. 6, *E′*). This patch of cells has all the appearance of a sensory epithelium. There are several such patches, less striking, about the various flaps and folds of the head.

The regular glands are rather numerous, and are found in all regions of the skin. They seem to be a little more numerous on the sides of the segments above the bases of the parapodia, and on the ventral surface to the right and left of the median groove. These cells have a characteristic shape resembling a truncated cone, the larger diameter being distal. The cell-wall, nucleus, and cytoplasm are quite distinct, and the latter has a very characteristic reticulated structure which is shown in Fig. 15.

The third type of epidermal cells—the "twisted" gland cells—occur in most parts of the epidermis, and are rather numerous. They occur in the ordinary regions of the body singly or in small groups separated by one or more epithelial cells; but they are often in clusters of 4 or 5 or more on the tentacles and cirri. In general they are more numerous on the exposed parts of the body, and much less so in the depressions, though they are abundant at the lips of such grooves. They are somewhat flask-shaped, usually with

irregular surface depressions that give the appearance of a spiral twist (Fig. 22). They vary considerably in size. Each cell has a distinct neck, and opens to the exterior through a pore in the cuticle. The reticulum is conspicuous throughout the cell. Usually these cells stain densely, especially at the wall. The internal reticulations are very much less stained. Often the glands show only a slight, ghostly staining, suggesting a difference of physiological state. The distribution, and apparently empty condition of many of the glands suggest that they may be the phosphorescent organs; though of this the authors have no final proof. In the dorsal region of a male specimen these glands show a somewhat different structure, as appears in Fig. 22a., *Sg*. Here the structure is of a much divided tubular sort. Their distribution and general relations, however, mark them as identical with the twisted cells.

The muscles of the body-wall present no significant departure from the condition described for other nereidiform worms. The outer circular layers give rise to acicular muscle fibers and to fan-shaped oblique fibres concerned in the motions of the parapodia. The longitudinal muscles are massed in four heavy bands—two dorsal and two ventral. They too give off tracts of fibres to the parapodia. The general relations of the muscles are very well shown in Figs. 20, 21. The muscles are unstriate.

The Alimentary Canal.

The alimentary canal is a nearly straight tube running the length of the body from the mouth to the anus. It is in no wise degenerate, as in some of the Syllids; but is functional throughout its course. Five regions may be distinguished, the last four of which are sharply differentiated from each other: (1) buccal cavity; (2) pharynx; (3) esophagus; (4) gizzard; (5) intestine.

A number of features, both embryonic and histological, seem to suggest the point of union of gizzard and intestine as the beginning of the mesenteron. There is a cuticular lining with very pronounced developments as far as the anterior end of the gizzard, and in less degree throughout its extent. It will be seen that the chief differentiations of the tract are in the stomodaeum and that the mesenteron is quite uniform in size and structure.

Mouth and Pharynx.

The first two regions, the buccal cavity and the pharynx, constitute an introvert. When withdrawn the buccal cavity occupies the peristomium, and the pharynx extends from the first setigerous segment to the seventh. When fully everted the buccal region is turned wrong side out, and the terminal opening is directly into the muscular pharynx, which is pulled forward its full length so that its posterior end is in the first or second setigerous segment. Compare Figs. 2 and 3.

The oral opening, when the introvert is withdrawn, presents a lobed margin of which the first setigerous segment furnishes the posterior ventral portion—a kind of lower lip (Fig. 5). The first and second peristomial segments form the remainder of the boundary to the mouth. The ventral floor of the buccal cavity is glandular (Fig. 2; 14, *g.*) while the sides are merely transitional from the outside to the pharynx. There is also a deep glandular fold from the dorsal wall of the cavity at the anterior margin of the pharynx (Figs. 1, 2, *O*).

The anterior part of the pharynx is very thick and muscular, but the posterior one-third, or thereabouts, is thin and pliable. It is this latter region that allows the adjustment of the phaynx to the body space when it is withdrawn into the body. This thin zone is thrown into a backward directed fold into the coelom, dorsal to the anterior end of the esophagus (Figs. 2, 3, *Ph'*.) The anterior end of the esophagus comes to lie within the lumen of the posterior part of the pharynx. The wall of the pharynx is composed of (1) the internal cuticle, (2) the epithelial lining which secretes the cuticle, (3) a thick muscular coat, and (4) the peritoneum.

The cuticle is continuous with that of the skin and similar to it in structure, but presents modifications in certain regions. It is thickened into minute conical denticles over a large portion of the pharyngeal surface (Figs. 2; 14, *dt.*). In the dorsal part the denticles begin with the mouth and extend about one-third of the length of the pharynx. In the ventral floor they begin at the posterior edge of the glandular region (Fig. 14) and cover perhaps two-thirds of the floor back of that point. The glands and the denticles do not occur together.

The epithelial layer of the pharynx is thrown into a series of longitudinal folds, somewhat irregular at first, but becoming more definite posteriorly. One of these in the dorsal part of the pharynx has almost the definiteness of form of the typhlosole of the intestine of the earthworm (Fig. 18). The epidermal cells of the posterior portion of the thick muscular region of the pharynx are conspicuously glandular. In the thin region, that forms the flexure in introversion, the cells revert more nearly to the ordinary type of epithelium.

The muscular layer is the most conspicuous one in the wall of the pharynx. It consists of a complex of circular, longitudinal, and radial or oblique fibres. In a longitudinal section of the organ the circular fibres show themselves to be arranged on both sides of sheets, which radiate from the lumen outward not at right angles to the lumen, but in positions depending on the degree of inversion. The circular fibres appear to dominate in this organ, but it is much less easy to distinguish the various layers here than in any other part of the body. Indeed it is easy to see that the layers are not as independent as elsewhere, and intermix to a greater degree.

The Esophagus.

The esophagus when withdrawn occupies segments 8 to 11. At its anterior margin occurs a ring of cuticular teeth which give the name to the genus. In the ventral floor there is a row of six of these, closely appressed, uniform in size, conical in form, and curved slightly backward. On the lateral walls near the dorsal part, and arching over so as to engage the ventral teeth, is a somewhat larger recurved tooth on either side of the lumen. In introversion the dorsal ridge of the pharynx is pressed in between these lateral teeth (see Fig. 18, *Df.*). It is very difficult to get satisfactory sections in the region of the teeth.

From within outward the layers in the wall of the esophagus are: The very much thickened cuticle, comprising about one-third the thickness of the whole wall; the columnar epithelium; the layer of circular muscles about the thickness of the epithelium; the longitudinal muscles, two-fifths the total thickness of the wall; and the thin peritoneum.

The cuticular layer is thicker in the esophagus than at any other

part of the body. It stains densely except at the very outer margin and shows a clear striate structure, the striations running perpendicular to the surface. While the teeth are to be looked upon as special thickenings of the cuticle, there is a sharp demarcation between this layer and them (Fig. 23.)

The arrangement and character of the muscles in the region of the esophagus shows that they are not so much concerned with the mere action of the esophagus itself as with the larger problem of introversion and eversion, and of the manipulation of the teeth at the anterior end of the esophagus. It is not the purpose of this paper to trace out the course and value of the various muscular tracts; but an examination of the various figures will suggest the role of some of the muscles massed about the anterior end of the esophagus. They bring the latter organ into proper relation to the processes being initiated by the action of the pharynx, as well as furnish a point of attachment for some of the elements engaged in retraction and protrusion. The thickened cuticle of the esophagus is undoubtedly for this purpose, and for the added purpose of keeping the esophagus open and functional during the various vigorous changes of form and position of the introvert.

The Gizzard.

The gizzard or stomach is a highly developed structure immediately following the esophagus and sharply demarcated from it. It extends normally from about the 12th setigerous segment to the 21st. It practically fills the body cavity in these segments. It is of uniform size except where it tapers off rather abruptly to join the esophagus and the intestine. It is elliptical in cross-section; and the lumen is in the form of a long narrow slit, the sides of which are nearly parallel. This slit-like lumen divides the organ into symmetrical halves, whose walls are very thick except in the part opposite the edges of the lumen. Here it is not more than 1-5 the usual thickness. Apparently the morphological position of the slit is dorsi-ventral; but the whole organ may be rotated until it has a right left position. From a surface view, or in excentric longitudinal (tangential) section, the whole wall of the organ is seen to be crossed by a series of fine parallel lines running transverse to the organ. The band-like spaces between these lines are divided into numerous

angular areas of nearly uniform shape and size. The whole presents a remarkably regular and interesting pattern (Fig. 25). Haswell (1886) has shown in his study of various species of Syllids that the wall of the gizzard is a highly complex muscular organ; and is not, as has long been supposed, a glandular one, at all. These studies confirm his conclusion in all essential particulars.

In detail, the wall of the gizzard, from within outward, shows the following regions: (1) the epithelium with its very thin secretion of cuticula; (2) a very much reduced muscular layer (Fig. 24, *mi.*) which contains internally one thickness of circular fibrès and just without this a similar single thickness of longitudinal fibres; (3) a thick zone made up of muscular elements which show chiefly as radiating columns in a transverse section or in longitudinal sections radial to the organ (Figs. 21; 2, V; 24, *Col.*); (4) a thin layer of elements (Fig. 24, *mo.*) which certainly contains circular muscular fibres, and according to Haswell contains longitudinal fibres also; (5) the thin peritoneal layer.

None of these layers call for special comment with the exception of the thick muscular layer which furnishes the main body of the wall of the gizzard.

A view when the gizzard is cut longitudinally, in such a way as to display the radial elements uncut, would be illustrated by Fig. 2, V, at the left-hand side of the figure. Such a view shows three chief topographic features: (1) a series of fibrous columns passing from the thin inner muscular sheet to the outer; and (2) lying between these, open spaces somewhat shorter than the columns and tapering toward both ends; and (3) in the outer portion of these open spaces, tapering objects, thicker at the outer ends, which extend from the outer wall about one-half the way to the lumen.

Study of these objects in other sections (see Figs. 2; 24) shows the radiating columns to be muscle fibres extending the whole thickness of the wall of the gizzard. They appear as columns in the transverse section of the gizzard also (Fig. 21, 3) but do not have such well-developed spaces between them. The tapering objects extending inward between the columns present a granular appearance and are in fact annular muscle fibres cut cross-wise. They form the transverse lines that show in a tangential section, such as is

seen in Fig. 25,*Cb*. They are in reality thin, wedge-like bands of muscle fibres that encircle the gizzard and separate the radial columns into successive circular zones, also shown in Fig. 26, *Cb*. Only the outer halves of the columns are thus divided, since the circular bands extend only part way to the lumen. In the cross-section of the gizzard these circular bands present their fibres in longitudinal view. They show dimly (Fig. 21, 2) in such sections outside the wavy line which appears midway the columns (Figs. 21, 24). These circular fibres are of the usual unstriate type and coalesce with the circular sheet of fibres of the inner muscular layer at the two edges of the lumen of the gizzard (Fig. 21, *Ra.*), and only there. The wavy line seen in Fig. 24 about midway on the columns seems to be the mark of the union of the inner thin edge of the circular band of fibres with the adjacent radial columns.

The histology of the radial columns has been worked out in much detail by Haswell for several Syllids. The differences between the conditions in *O. enopla* and those described by him are of minor moment. The individual fibrils run the length of the columns and are undoubtedly made up of alternate light and dark bands, such as are seen in typical cross-striate muscles. Haswell remarks that the striations found in these fibres are more strongly marked than in any crustacean or insect he had examined.

Considered as a whole, each one of these radiating columns of cross-striate muscle fibrils is made up longitudinally of two symmetrical halves hollowed out on their inner faces in such a way as almost to surround a cavity. This cavity is small and closely surrounded near the inner end of the column, as seen in cross-section (Fig. 27, f); but in cross-sections further from the lumen, the space between the two halves becomes larger, and is less completely surrounded by the muscle fibres. In the outer half of its course the halves of a given column fall on different sides of one of the circular bands of muscles referred to above. See Fig. 26, which represents a cross section of a group of the columns about two-thirds of the way toward the outer surface, and shows the circular muscles separating the triangular halves of the columns and thus throwing them into a band back to back with the nearby halves of the next row of columns. Figure 25 shows

the relation of the parts just as close to the outer end of the columns as a section can be made. In this figure the outer ends of the half-columns included between two of the bands of circular fibres are shown almost to run together into a continuous zig-zag sheet. At this level the space between the circular band of unstriate fibres (Fig. 25, *Cb.*) and the adjacent zone of the radial columns (Fig. 25, *col.*) is occupied by a mass of granular nucleated protoplasm (Fig. 25, *n*). This protoplasm extends only a short distance down the columns, as appears in Fig. 28, n., which shows a section perpendicular to that in Fig. 25.

In brief summary, then, the gizzard is a complex muscular organ with an outer and inner sheet of unstriate fibres; a parallel series of thin bands of annular unstriate muscles, whose outermost fibres are in close relation to the external muscular layer, and extends inward as a band from the outer muscular sheet only about one-half the thickness of the whole wall, except that it reaches entirely to the inner muscular sheet at the angles of the lumen where the wall is thinnest and there gives off fibres which unite with it; and a series of radial columns of striate muscle fibres, each column of which is made of two trough-like halves whose concave sides are apposed in such a way as to make a conical cavity with its largest diameter at the outer end.

From the point of view of histogenesis the most interesting things about the gizzard are this mixture of striate and unstriate fibres in the single organ, and the evidence that the central cavity of the radial columns presents at the outer end a remnant of the granular protoplasm from which the muscular fibrils were differentiated. Each of these hollow columns is a simple muscular organ, in which the contractile elements are the product of the single multinucleate mass of protoplasm occupying its core and it is differentiated progressively toward the periphery, as is suggested by the last position of the nucleated protoplasm (Fig. 28 *n.*). The embryonic character of the mature fibres, and the simplicity of the relation of the fibres in the organ mark the organism as one that would well repay study upon the ontogenetic differentiation of the muscles of the gizzard.

The Intestine.

The intestine is a straight tube passing with nearly uniform character, and with gradually diminishing size, to the anal opening. It has the usual constrictions between the segments, with sacculations almost amounting to diverticula within the segments. The epithelial lining has the usual variety of columnar cells. Those in the posterior part of the tract are heavily ciliated. Both circular and longitudinal fibres may be found, but they do not form a definite or continuous sheet of tissue. Fig. 20 illustrates a cross section of the body, in the intestinal region, which includes a dissepiment. The intestine is sharply constricted; the layer of longitudinal muscle fibres appears clearly just outside the entoderm; and a thick zone of circular fibres outside this shows a clear anastomosis with the circular fibres of the body wall in both dorsal and ventral regions. The distribution of oblique muscle fibres in the dissepiment is also shown—the origin being in the ventral region on either side the nerve cord and passing out fan-wise to the muscular layers of the dorso-lateral walls. At least some of these fibres run into the circular muscular sheet in being inserted.

The only noteworthy differentiations in its length are the shallow proctodeum, and the valvular enlargement of the intestine at its junction with the gizzard (Fig. 4, *v.*). At the beginning of the intestine there is a special annular or sphincter group of muscle fibres (Fig. 4, *S*).

The Circulatory System.

The blood vessels agree with those described as characterizing the Syllids generally, and call for little special discussion. The dorsal vessel is small and thick-walled as compared with the ventral. The dorsal vessel is imbedded in the wall of the intestine in an interesting way thru a part of its course—the peritoneal membrane inclosing both in one sheath (Figs. 17; 29). Segmental vessels arise from both the dorsal and ventral longitudinal vessels and run outward on the anterior face of each dissepiment.

The Excretory System.

The nephridia are quite large organs in this worm in comparison with the size of the body. This is due in the female to the liberal

glandular portion. The nephridia apparently occur in all the setigerous segments of the body beginning with the very first—which is also the last segment of the peristomium.

In the male the tubular ciliated portion of the nephridium is much larger than in the female, and the glandular part appears less massive (Fig. 11, *N.*, *G.*). In the sections of a female, whose cavity was filled with eggs in such a way as to indicate that ovulation had not occurred, the tubular part of the nephridia was so compressed and displaced as to preclude the possibility that they could be used for the discharge of eggs, at least at the beginning of ovulation. In the male on the contrary there is abundant evidence that these organs are in an hypertrophied condition, and probably they function as vasa deferentia. They have large lumens, and protrude well into the middle of the body.

Genital Products.

As in other polychetes the eggs and sperm are produced by proliferation from the coelomic peritoneum. They are found in all the full-sized segments of the body, beginning about the 19th or 20th setigerous segment. Ripe eggs were found in sections two or three segments anterior to the union of gizzard and intestine. Fig. 30 shows a cross-section of a female which has not deposited any of her eggs. In this case the eggs are so numerous that the segment is stretched until the body wall is very thin. The eggs occupy every available cavity. As has been indicated it appears to the writers that the ova could not use the nephridia in this case, but must escape by rupture of the body wall.

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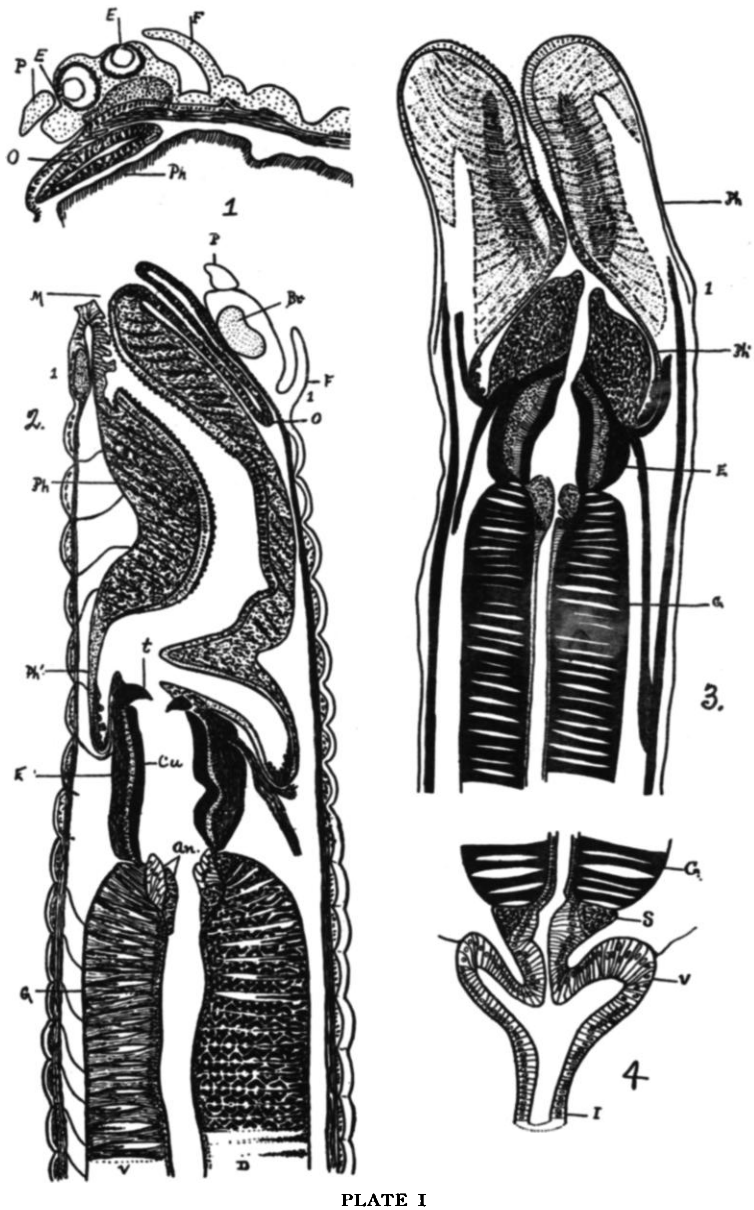

PLATE I

EXPLANATION OF PLATES

Plate I

Fig. 1. A para-sagittal section of the dorsal part of the head. Diagrammatic. *E,* the pupils of the eyes (see also Fig. 7); *F,* flap of peristomium (see also Fig. 6); *O,* a glandular fold at the dorsal anterior edge of the pharynx (see also Fig. 2); *P,* palp; *Ph,* pharynx.

Fig. 2. A sagittal section of the head and anterior segments, with the introvert withdrawn. 1, the last peristomial (first setigerous) segment; *an,* an annular organ in the cardiac opening of the gizzard, consisting of modified epithelium and circular muscle fibres; *Br.* brain; *Cu,* cuticula of the esophagus *(E); F,* a flap projecting forward from the 3rd peristomial segment (see also Figs. 1 and 6); *G,* gizzard, in which the dorsal *(D)* and ventral *(V)* walls are cut in different relation to the elements composing the wall; *M.* mouth; *O,* a thin-walled glandular pocket at the anterior, dorsal edge of the pharynx; *P,* palp; *Ph,* pharynx, with thick muscular wall; *Ph',* thin-walled, flexible portion of pharynx; *t,* cuticular teeth in anterior margin of esophagus. ×40.

Fig. 3. A frontal section thru head and anterior segments, with the introvert protruded. Lettering as in Fig. 2. ×40.

Fig. 4. Longitudinal section at junction of gizzard and intestine. *G,* gizzard; *I,* intestine; *S,* sphincter muscle at beginning of intestine; *V,* valvular enlargement at anterior end of intestine. ×40.

Plate II

Fig. 5. Ventral view of the head; *l*, lateral tentacle of the prostomium; *m*, median tentacle; *P*, palpus; 1, 2, 3, the peristomial tentacles or cirri. The lower lip is shown to be an anterior projection of the first setigerous segment. ×15.

Fig. 6. Longitudinal section thru dorsal body-wall immediately in front of 3rd peristomial (first setigerous) segment, B, brain; E, epithelium; *E'*, the thickened sensory epithelium in front of the peristomial flap *(F)*. ×300.

Fig. 7. Eye. A median section of anterior eye thru pupil. *Cu*, cuticula; *E*, epithelium; *Le*, lens; *o. n.*, optic nerve; *Pe*, pedicel of the lens; *Pg*, pigment layer of the retina; *r*, rods, or layer formed by inner ends of retinal cells; *R*, retinal cells, deeper portion containing nuclei. ×330.

Fig. 8. Ommatidium. *C*, the nucleated part of the cell; *F*, fibre; *Pg*, pigment, which collectively makes the pigment cup of the eye; *r*, the rod or inner end of cell. ×500.

Fig. 9. Setae-sac of dorsal bristles, cut in the long axis of the setae. *A*, aciculum; *c*, bristle cell, from which the bristles arise; *m*, basement mebrane; *s*, seta (see also Fig. 16). ×125.

Fig. 10. Cross-section of two parapodia showing both the dorsal and ventral bristle sacs cut across the long axis of the setae. *A*, acicula (the smaller light objects are the setae); *Ci*, dorsal cirrus; *n*, nephridium; *S'*, ventral seta-sac; *S"*, dorsal sac, with the swimming bristles in two parallel rows. The darker dots show muscular elements. ×50.

Fig. 11. Cross-section of a segment in the mid-region of the body of a male. *G*, glandular part of nephridium; *N*, the tubular portion of nephridium, much enlarged and used as sperm-ducts; *T*, the twisted gland cells (see Fig. 22) numerous in the dorsal body wall. ×50.

Plate III

Fig. 12. Dorsal view of head and anterior body segments. *Ey*, eyes, occurring in pairs on flaps; *L*, lateral tentacles of the prostomium; *M*, median tentacle; *P*, palpus; *Ph*, introvert protruded; 1, 2, 3, the tentacles of the three peristomial segments. ×15.

Fig. 13. Lateral view of the head. Lettering as in Fig. 12. ×15.

Fig. 14. Sagittal section thru buccal cavity, showing beginning of the pharynx. *D*, dorsal; *V*, ventral, *dt*, conical denticles of cuticula in wall of pharynx; *g*, a patch of glandular cells in floor of mouth; *Ph*, lumen of pharyx.

Fig. 15. Gland cells of epidermis. *C*, cuticula; *E*, epithelium; *g*, gland cell showing characteristic inner reticulated protoplasm and outer striated protoplasm. ×600.

Fig. 16. Setae. *D*, the dorsal, capilliform, swimming setae of the mid-body region; *V*, the ventral jointed setae, occurring the whole length of the body.

Fig. 17. Cross-section of the body in the mid-region of body. *Ci*, dorsal cirrus; *I*, lumen of intestine; *O*, ova in body cavity. ×50.

Plate IV

Fig. 18. Cross-section of pharynx and esophagus, with introvert withdrawn. *E*, muscular wall of the esophagus, showing the lateral mass of muscular fibres connected with the tooth apparatus; *ep*, epithelial layer that secretes the ventral teeth; *Df*, a longitudinal, dorsal fold of the pharynx that invades the front of the esophagus in introversion; *Ph*, muscular wall of the pharynx. ×65.

Fig. 19. Similar cross-section a little anterior to Fig. 18. ×65.

Fig. 20. Cross-section in mid-region of body, including a dissepiment *(Di)*. 1, dorsal ramus of notopodium, bearing dorsal cirrus *(Ci)*; 2, ventral ramus of notopodium, bearing swimming bristles supported by aciculum; 3, dorsal ramus of neuropodium, bearing bristles and acicula; 4, ventral ramus of neuropodium with no appendages. ×50.

Fig. 21. Cross-section of body thru the gizzard. *A*, aciculum; *Ci*, dorsal cirrus; m^1, layer of circular muscles of body wall; m^2, longitudinal muscles; *Ra*, raphe where there is an anastomosis of the fibres of the annular band of muscle fibres (2) with the innermost layer of the gizzard. The numerals indicate three successive zones of elements in the wall: 1, the peritoneum and thin outer muscle layer; 2, annular bands of fibres, much flattened in the direction of the long axis of the animal suggested by the broken lines; 3, muscular columns which make up the bulk of the wall of the organ. Within this is a thin layer consisting of muscles, epithelium, and cuticula. ×65.

Fig. 22. "Twisted" glands (phosphorescent?) from epidermis of female. *Po*, pore in cuticula; *Sg*, the gland with constrictions. ×680.

Fig. 22a. Similar glands in the dorsal epithelium of a male specimen. ×680.

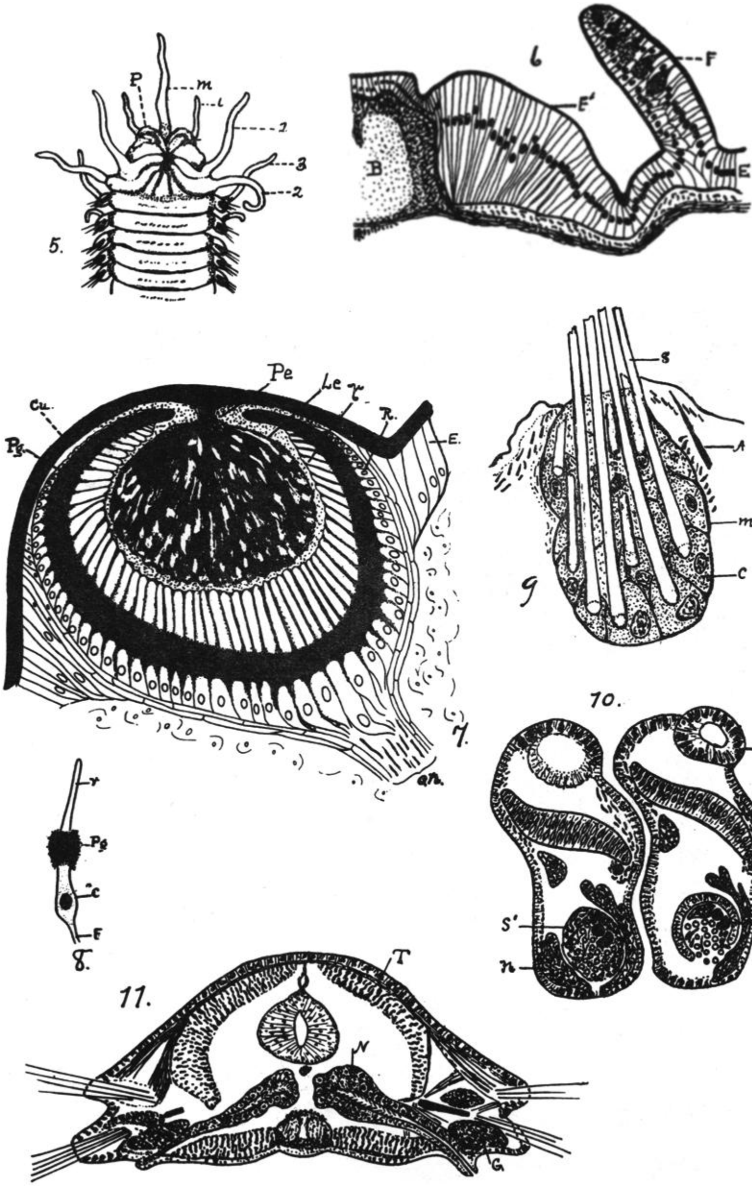

PLATE II

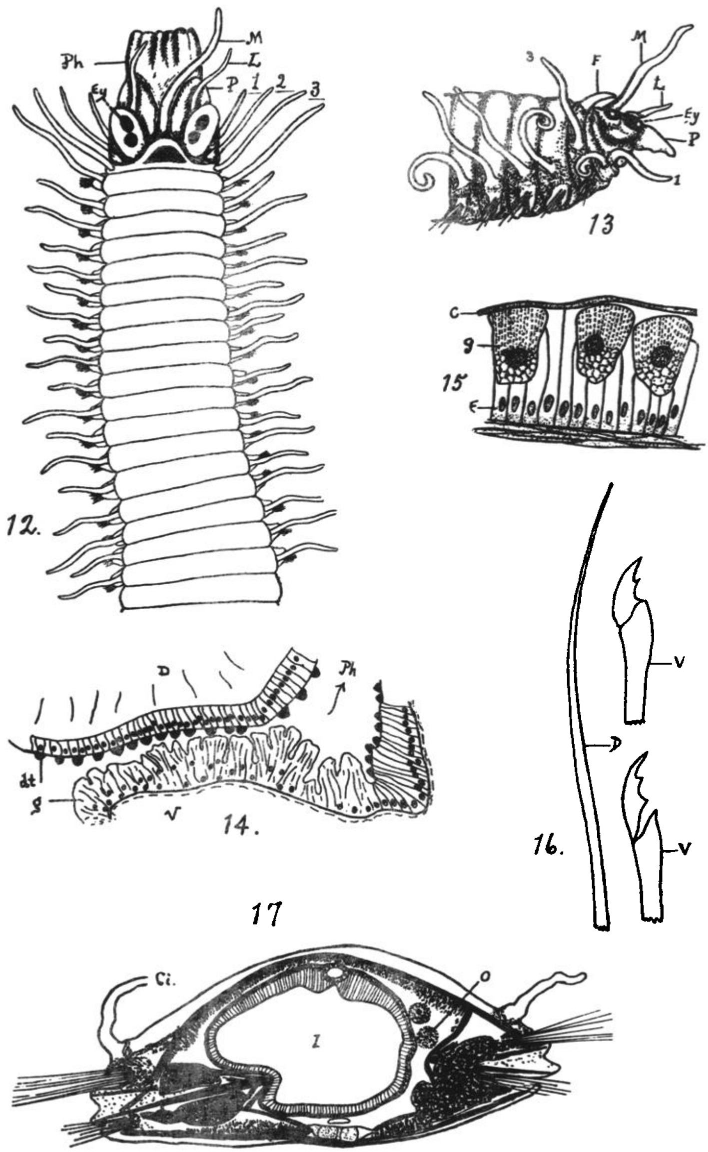

PLATE III

Plate V

Fig. 23. Detail of ventral floor of esophagus, longitudinal section, in region of teeth. *Cu,* cuticula lining esophagus; *Ep,* epithelial layer; *g,* glandular epithelium in the thin portion of pharynx; *t,* one of the ventral teeth.

Fig. 24. Two muscle columns of the gizzard, taken from transverse section of that organ (see Fig. 21). Lettering in figures 24-28: *cb,* "circular band," a thin sheet of muscle whose fibres encircle the organ; *col,* the radial muscular columns whose fibres radiate from the lumen; *f,* a fissure separating the halves of one column; *mi,* thin inner muscular layer; *mo,* a thin outer muscular layer; *n,* nucleated protoplasm between the outer ends of the half-columns.

Fig. 25. Section perpendicular to 24, transverse to the columns and tangential to gizzard, just as near the outer surface as possible. ×320.

Fig. 26. Section transverse to the columns (parallel with 25), at a deeper level. ×160.

Fig. 27. Section parallel with 24 and 25, transverse to the columns at their inner end). ×160.

Fig. 28. Longitudinal section of columns (outer end) at right angle to Fig. 24, showing them as they appear in longitudinal section of the gizzard. ×160.

Fig. 29. Dorsal wall of intestinal tract showing relation of dorsal blood vessel to it. *cil,* cilia; *d,* dorsal blood vessel; *ep,* epithelial lining of digestive tract; *L,* lumen of blood vessel. ×360.

Fig. 30. Cross-section from mid-body region of a female in which ovulation has not commenced. *N,* glandular part of nephridium; *O,* ova; *W,* the much stretched and thinned dermo-muscular wall. ×40.

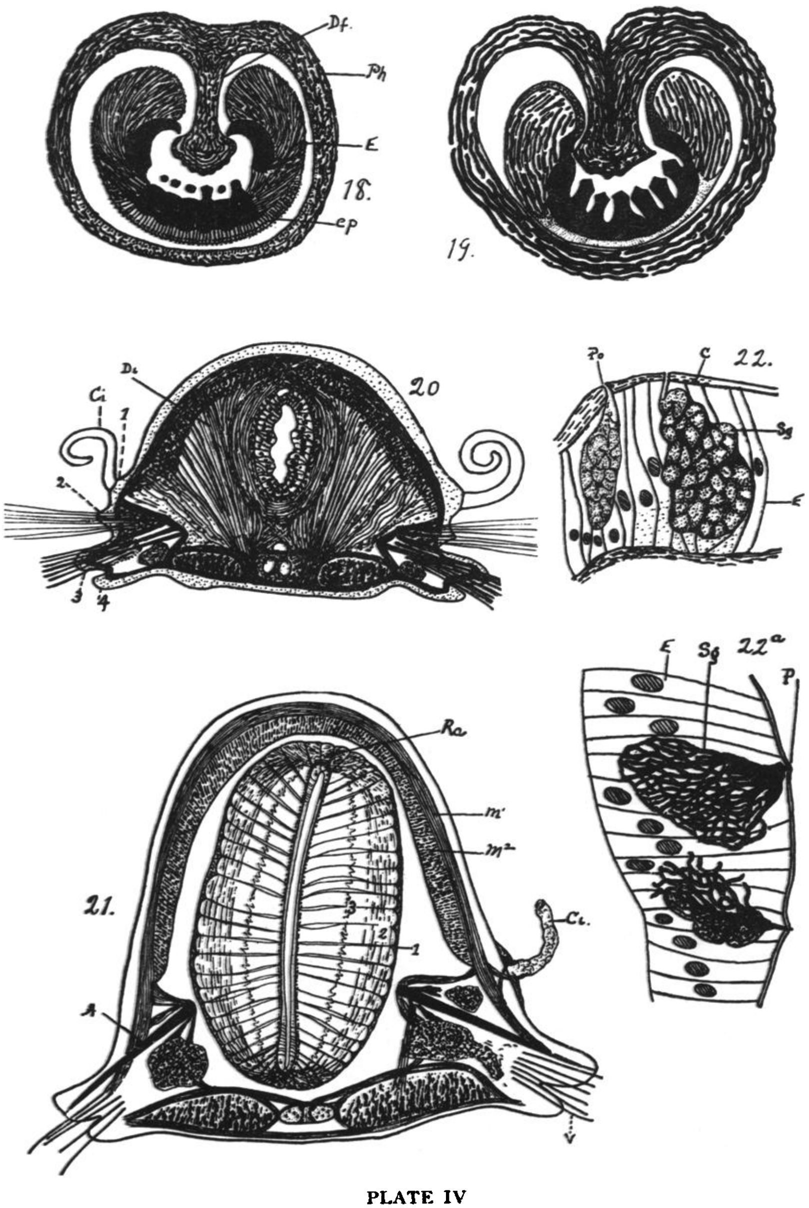
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PLATE IV

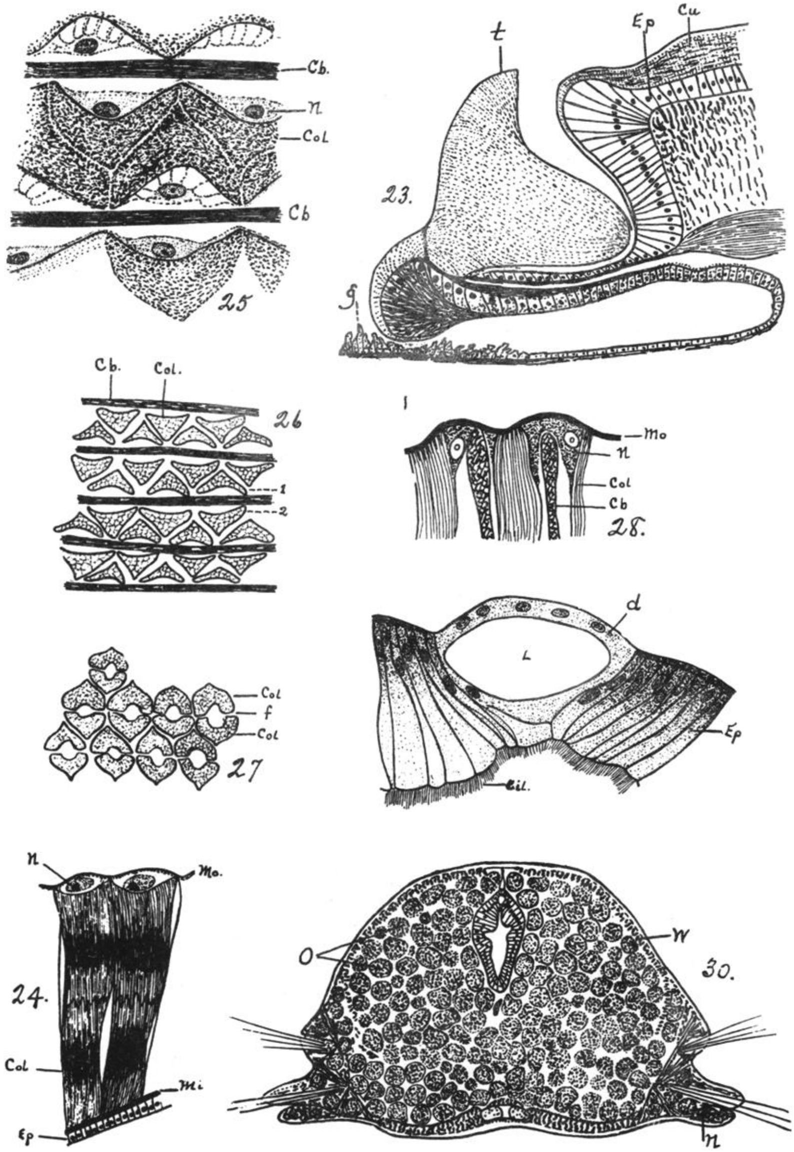
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PLATE V